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银杏雌性生殖器官的形态学本质及其系统学意义

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A NEW MORPHOLOGICAL INTERPRETATION OF THE FEMALE REPRODUCTIVE ORGANS IN *GINKGO BILOBA* L., WITH A PHYLOGENETIC CONSIDERATION ON GYMNOSPERMS

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Summary The ovuliferous structure of *Ginkgo biloba* L. has been variously interpreted morphologically. As a result the systematic position and the relationship with other gymnosperms of this ancestral gymnosperm have long been under dispute. In the present paper, a brief survey of the main views as to the nature of the ovuliferous structure is given. Based on morphological and teratological data previously reported, a new interpretation is proposed. The essential points are summarized as follows:

1. In morphological essence, a fertile dwarf shoot with some ovuliferous structures in *Ginkgo biloba* L. might as a whole be nothing but a megasporophyll strobilus (female cone), which is shared actually by all the conifers in the gymnosperms. The fertile dwarf shoot has appearance extremely similar to that of the vegetative dwarf shoot, suggesting that in *Ginkgo biloba* L. the vegetative organs and the reproductive organs have not been yet well differentiated, and thus its megasporophyll strobilus might represent one of the most primitive compound strobilus types.

2. In *Ginkgo biloba*, the ovuliferous structure borne in the axil of a scale leaf (sometimes a normal leaf) on the dwarf shoot, together with the scale leaf itself, might be the homogenous organ corresponding to the bract-scale and seed-scale complex of the compound female strobilus of the typical conifers. The

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complex is a relatively isolated reproductive unit on the strobilus. The normal leaves and the scale leaves on the dwarf shoot might be equivalent to the bract-scales in the typical cones, though the normal leaves still retain the vegetative nature as the foliage leaves on the vegetative shoot. The stalk bearing ovules at its top might be equivalent to a seed-scale of the typical cones.

3. The megasporophyll strobilus in *Ginkgo biloba*, namely a whole fertile dwarf shoot as mentioned above, seems to show much more primitive characteristics than those of typical conifers. In this plant it is very difficult to distinguish the fertile dwarf shoot from the common vegetative dwarf shoot before reproduction time. Moreover, its megasporophyll strobilus often exhibits more atavistic abnormalities than those of other conifers. All the evidence indicates that the primitive ancestor of conifers might have had the fertile organs which might be of basically identical morphology as vegetative shoots, except that in the fertile organs there might exist numerous fertile leaves bearing one or many ovules.

4. The longer stalk of the ovuliferous structure in *Ginkgo biloba* might have come from mainly a secondary elongation growth of the seed scale, and only a little part of it might be the remains of the original shoot. The fork structure bearing ovules at the top of the stalk might be the rudementary part of the petioles of the only two extremely reduced megasporophylls. The collar around the base of the ovule might be a secondary protective structure.

5. A correct morphological interpretation of the female strobilus in *Ginkgo biloba* is doubtless of important significance for our better understanding of the evolution of the female reproductive organs in conifers. According to our interpretation mentioned above, together with the concept of the bractscale and seed-scale complex proposed in the present paper, which is mainly based on the concept of the seed-scale complex propose by Florin, here we put forward an evolutionary theory of the bract-scale and seed-scale complex. According to this theory, the female reproductive organs of the ancestral conifers should be very similar, as mentioned above, to the sterile foliage shoot except that the former might have some fertile leaves which could produce ovules at reproduction time. This ancestral female reproductive organ type might have had evolved towards two directions and thus formed two main evolutionary lines. One is represented by the genus *Cycas* and we may call it the *Cycas* Evolutionary Line (C-line), in which the megasporophyll strobilus is monopodial, with the fertile leaves and sterile bracts occurring directly on the main axis. The Cycadaceae is the only living gymnosperm member along this evolutionary line. The second line is represented by all the conifers including *Ginkgo*, which all have the structure of the bract-scale and seed-scale complex, and thus we called it the "Bract-scale and Seed-scale Complex Evolutionary Line" (BS-line).

The members along this line have multipodial female strobilus, i. e. compound strobilus. On the main axis occur some sterile vegetative bracts. In the axils of some or most of the bracts occur the seed-scales. The seed-scales are actually the remains of the extremely, or smetimes completely reduced fertile shoots. Each part of the bract-scale and seed-scale complex and the main axis of the strobilus could have undergone independent or correlated changes, and thus have had formed various types of strobilus which are found in the living conifers.

6. Our theory on the evolution of the bract-scale and seed-scale complex seems to support the division of all the gymnosperms into two major groups as proposed by Chamberlain, and is also in favour of the placement of Ginkgo biloba into the conifers as the most primitive member along BS-line.

7. Based on their similar morphological characters, it can be considered that *Ginkgo biloba* might have close relationships with the Nageiaceae, Ephedraceae, Welwitschiaceae and Araucariaceae. All these groups have multinerved leaves without costa. These living gymnosperms might have a more direct relationship with the ancestral cordaites.

Key word *Ginkgo biloba* L; Female reproductive organ; Bract-scale and seed-scale complex; Systematics of gymnosperms

摘要 关于古老裸子植物银杏 *Ginkgo biloba* L. 雌性生殖器官形态学本质的问题争论很多，因此这一类群的分类位置尚存争议。本文进一步发展了 Florin 提出的"种鳞复合体(Seed-scale complex)"概念，提出解释裸子植物生殖器官形态演化的"苞鳞－种鳞复合体(Bract-scale and seed-scale complex)概念和演化理论，并试图用以解释银杏的生殖器官形态学本质和裸子植物系统发育的有关问题。由银杏着生胚珠的结构(Ovuliferous structure)生于可育短枝上鳞状叶叶腋的事实，赞同该结构为次级轴性(枝性)性质，提出该次级轴性结构及连同下部的鳞状叶相当于裸子植物大部分类群所具有的苞鳞 － 种鳞复合体(Bract-scale and seed-scale complex)，并保留了较多的原始古老性质，可能代表着苞鳞 － 种鳞复合体较原始的形态式样。该结构的鳞状叶与可育短枝上正常的营养叶均为不育苞片的性质，鳞状叶叶腋生出的长柄则是次级轴性结构的次生性伸长，长柄上部二分叉的着生胚珠结构相当于该次级轴性器官仅存的极度退化的二枚可育叶性器官，而整个可育短枝相当于一个分化程度很低的复合大孢子叶球。银杏生殖器官中的某些性状与苏铁十分相似，但由于苞鳞 － 种鳞复合体的出现，标志着这一类群已远较苏铁特化，并应与所有具苞鳞－种鳞复合体的类群在同一条演化线上，即苞鳞 － 种鳞复合体演化线(Bract-scale and seed-scale complex evolutionary line, BS-line)，而不具苞鳞 － 种鳞复合体的苏铁类(*Cycas*)则构成裸子植物中的苏铁演化线(*Cycas* evolutionary line, C-line)。银杏大孢子叶球的式样，可能代表着裸子植物一种早期的原始大苞子叶球式样，为古裸子植物不甚分化的可育枝条向高度压缩和变态的可育枝条(苞鳞 － 种鳞复合体及典型的球果)演化的一种中间过渡式样。

关键词 银杏；雌性生殖器官；苞鳞 － 种鳞复合体；裸子植物系统学

(待续 to be continued)